TRANSACTIONS
OF
American Microscopical Society
(Published in Quarterly Instalments)
Vol. XXXVIII JULY, 1919 No. 3

FURTHER STUDIES ON NORTH AMERICAN MESENCHYTRAEIDS (OLIGOCHAETA)*

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Part I. Mesenchytraeus hydrius n. sp.

Habitat

The following description is based upon a collection of enchytraeids made by Mr. J. B. Flett in the Mt. Rainier National Park, June 15, 1917, at an altitude of 3400 feet. This collection contained 91 specimens of which 24 were sexually mature and all apparently belonged to the same species, definite identification of the immature specimens being, of course, out of the question. They were found in slowly moving water in close proximity to melting snow, thus existing under conditions of low temperature. Mr. Flett reports that some of the specimens were taken from the sand in the bottom of the stream and that they offered considerable resistance when pulled from their burrows. They exhibit the usual crawling movements but dispersal is facilitated by their ability to loosen, or become loosened from their hold on the bottom and drift down stream. He also states that they

* Contribution from the Zoological Laboratory of the University of Michigan.

may possibly occur in the snow but since the color of the living specimens is so nearly that of the snow they would be overlooked easily. No information is available concerning the abundance of this form but judging from the number in this single collection, they evidently occur in large numbers in the Mt. Rainier habitat.

Identity

A study of this annelid based upon dissections and serial sections showed it to be a new representative of the genus *Mesenchytraeus* and another form belonging in the list of enchytraeids having the striking character of much enlarged and elongated spermathecae—a character which, as the writer (1916b, pp. 99–100; 1917a, p. 74) has already pointed out, seems to be restricted to North American species. The excellent state of preservation and the complete sexual maturity of 24 specimens made it possible to work out thoroughly all of the structural characters bearing on the identification of the species. In many respects, it resembles *Mes. setchelli* Eisen closely, the important differences being as follows: (1) larger number of setae per bundle; (2) distinctly larger number of somites; (3) much longer spermiducal funnel; (4) absence of sperm sacs; and (5) marked difference in the internal structure of the penial bulb; (6) crossed spermathecae.

External Morphology

The body of *Mes. hydrius* is cylindrical, elongate, smooth and approximately of the same diameter throughout except at the extremities and at the clitellar somites. The length (alcoholic specimens) varies from 17 to 24 mm. inclusive, and the maximum diameter (clitellar region) from 0.76 to 0.91 mm. inclusive. Externally, the segmentation is distinct only on the anteclitellar and the posterior portions of the body. Between inter-segmental grooves, the body surface is smooth, and free from secondary annulations of any sort. In the specimens examined, the somites vary in number from 82 to 97 inclusive. The well developed clitellum, occupying ⅓11–13, is continuous around the body except for a small area between and anterior to the penial bulbs where the clitellar thickening is lacking. The setae conform to the usual condition in the genus *Mesenchytraeus*, being distinctly sigmoid and arranged in four rows of fan-shaped bundles. In the lateral rows, the number varies from 4 to 7 inclusive:

in the ventral rows from 5 to 9 inclusive. Specialized setae are absent. The small, smooth, rounded prostomium carries the head pore near its tip. Color light yellow; pigmentation entirely absent, internally and externally.

Internal Morphology

Chloragog Cells. In the somites occupied by the elongated sperm-athecae, the chloragog cells are greatly reduced in number, being represented only by a few scattering cells or small groups of cells. These cells are, however, frequently much elongated. In the somites occupied by the long ovisac, more of the chloragog cells occur and while their ental extremities cover most of the surface of the alimentary tract, they are diverted from their usual radial arrangement, the free extremities being pushed around to the dorsal side. Somites caudad of the ovisac contain elongated chloragog cells arranged radially about the intestine.

Brain. The brain (Pl. XVII, Fig. 6) lies almost entirely in 1. It is about as long as wide, has parallel lateral margins, a truncated posterior margin, and a concave anterior margin. Two supporting strands extend to the body-wall.

Nephridia. A nephridium (Pl. XVII, Fig. 4, 5) consists of a small anteseptal region, little more than a mere nephrostome supported on a short, narrow pedicel, and a large, loosely constructed postseptal part of the usual mesenchytraeid type. The efferent duct is as long or a little longer than the entire nephridium and arises from the ventral surface of the postseptal part about midway of its length. There is no evidence of a reservoir at its ectal opening. There is considerable variation in the shape of the nephridia in the different parts of the body, although all conform to the general type described above.

Dorsal Blood-vessel. The dorsal blood-vessel arises in or very near 18. Distinct swellings occur in several somites just anterior to its origin.

Spermiducal Funnel. Two prominent spermiducal funnels (Pl. XVII, Fig. 7) lie in the clitellar region and, owing to their size and length, more than one somite is involved, one and sometimes both extending into 12. Each funnel is about seven times longer than the maximum diameter and fills most of the coelomic space in the somites occupied. Since the space within each somite is insufficient for both funnels, a

common arrangement is that in which one funnel, bent in a sigmoid figure, lies more or less transversely in one somite while the other extends longitudinally into the following somite, septum 11/12 being pushed caudad to septum 12/13. Usually the extremity of the funnel is reduced somewhat in diameter and terminates in a thin, flaring rim. The sperm duct is greatly coiled and massed in 13–14, the posterior coils lying in the ovisac.

Sperm Sacs and Ovisac. Definitely developed sperm sacs are not present. In some specimens, 11/12 is reflected caudad in such a way as to suggest the formation of incipient sperm sacs but such septal reflections do not extend beyond the confines of the clitellar somites. A large part of the coelom posterior to the clitellum is occupied by an extensive, unbranched ovisac which ends in 31–33.

Penial Bulb. The essential features of the "mesenchytraeid bulb" (Eisen, 1905, p. 7) are presented in the penial apparatus (Pl. XVII, Fig. 2, 3) of this species. In the retracted condition, each bulb surrounds a deep invagination which, in transverse section of the worm, appears as a bifurcating slit, thus forming a mesal compartment and an ectal compartment, both of similar shape and extent. This double chamber is lined throughout by a continuation of the external cuticula. The body of the bulb is firm, compact, and composed mainly of muscle tissue closely built together. A single layer of inner bulb cells surround the mesal side of the penial lumen but it composes only a small part of the mass of the organ. Peripheral gland cells are entirely lacking.

The ectal end of the sperm duct expands into a fusiform atrium which penetrates the bulb at a point on the mesal surface about mid-way between the ventral and the dorsal extremities. This atrium is composed of two portions, the larger fusiform portion lying in the coelom between the mesal surface of the penial bulb and the ectal end of the sperm duct proper, and the smaller, shorter portion enclosed within the body of the bulb. Structurally, the two parts are similar except that in the latter there is a much greater development of the longitudinal muscle-layer. At or very near the junction of these two parts the ducts from about five large, irregular, multicellular atrial glands enter the wall of the atrium but in the material at hand it has not been possible to follow these ducts further. The ducts of these atrial glands are difficult to follow, even outside the

atrium, and since the free ends of the glands lie about the base of the bulb, often in contact with it, they have, at first sight, the appearance of accessory glands. However, no true accessory glands were found.

Spermathecae. In form, size, and structure, the spermathecae (Pl. XVII, Fig. 1) resemble very closely those of *Mes. gelidus* Welch. In the specimens studied in this connection, each spermatheca is composed of three distinctly differentiated parts: the duct, the diverticula, and the ampulla. The duct is straight, slender, and uniform in diameter, extending caudo-mesad into the anterior part of 6. The ectal opening occurs laterad in 4/5 and is devoid of glands. At the junction of the duct and the ampulla, two, opposite, elongated, finger-like diverticula arise. These diverticula are, in the specimens examined, somewhat shorter than the duct. The ampulla composes the bulk of the spermatheca, extending caudad through the succeeding somites to the end of 10 and filling the greater part of the coelom in the somites involved. In fact, the ampulla is, in some cases, longer than the combined length of the somites through which it extends so that it may be doubled in varying degrees about the digestive tract. Constrictions at the septa are well marked but elsewhere the ampulla is, in the sexually mature specimens, distended with great masses of spermatozoa, the whole presenting something of a moniliform appearance when isolated from the body of the worm. The two ampullae of the animal are not symmetrical and may be slightly dissimilar in length but diversity, such as occurs in *Mes. gelidus* (Welch, 1916b, pp. 97–98), was not observed, both extending practically throughout the anteclitellar somites. In 10, the extremities of the ampullae may lie in very close contact with the wall of the digestive tract producing an apparent union with the latter which is very deceiving. Critical examination of both transverse and longitudinal sections through these regions has failed to reveal any true connection between the ampullae and the alimentary canal, the former ending blindly. Structurally, an ampulla is composed of two regions, a short ectal portion which adjoins the ental end of the duct and a very long ental part which constitutes the storage region of the organ. The ectal portion is rather thick-walled and the lining epithelium is thrown into a series of transverse folds while in the ental part the wall is reduced in thickness to the appearance of a mere membrane.

A remarkable peculiarity of these spermathecae appears in the fact that the right organ crosses to the left side of the body and the left organ to the right, the intersection occurring in the posterior part of 5 or the anterior part of 6, at about the level of the origin of the diverticula. This phenomenon is a constant feature in all of the specimens studied and may be regarded as a character of the species. In an earlier paper (1917a, p. 74), the writer pointed out a similar crossing of spermathecae in *Mes. altus* Welch, although in the latter case these organs pass each other about midway of the length of the greatly elongated ampullae. Such a crossing of spermathecae must have been coincident with the development of the organs.

Part II. Key to the Species of Mesenchytraeus Known to Occur in North America

There are two outstanding difficulties which hinder investigation of the Enchytraeidae, (1) the extremely scattered condition of the literature involved, and (2) the incomplete, fragmentary data on so many of the foreign species described in years past. It is indeed fortunate that practically all of the North American forms have been adequately treated and, so far as they are directly concerned, form a fairly satisfactory basis for work in this country. The world-wide roster of mesenchytraeid species presents at the present time about sixty names, although the standing of a few of them is a matter of uncertainty. Investigations indicate that the genus *Mesenchytraeus* is rather generously represented on our continent and with the hope of facilitating studies involving this genus, the writer has made several attempts to construct a usable key to all the known species but has found it a hopeless task, due to the fact that many of the Old World forms lack both uniformity and completeness in the description of essential details. In lieu of this more desirable but at present seemingly impossible treatment of the whole genus, the writer presents the following key to the identification of North American mesenchytraeids which may serve at least as a partial basis for work in this country.

1 (26) Spermathecae short, confined to 5 2

2 (3) Spermathecae without diverticula; no atrium; no accessory glands; 1 set of penial glands; 2 sperm sacs;

1 ovisac; spermathecae twisted at ectal openings; dorsal blood-vessel arising in 18 . . . . . *unalaskae* Eisen (See p. 185)

3 (2) Spermathecae with diverticula 4

4 (5) Spermathecae with 3 diverticula (occasionally 2); accessory glands present; 8 atrial glands; 1 sperm sac rudimentary, 1 fully developed sperm sac extending to 20, not enclosed in ovisac; sperm ducts extending to 18, only one enclosed within ovisac; ovisac extending to 22; dorsal blood-vessel arising in 12; enlarged setae in ventral bundles of 11 . . . . . *solifugus* (Emery)

5 (4) Spermathecae with two diverticula 6

6 (7) Sperm ducts absent; spermiducal funnels club-shaped and opening directly into penial pores without ducts; penial bulbs absent; no glands of any sort at ectal openings of spermiducal funnels; diverticula of spermathecae greatly reduced; 1 ovisac and 1 pair of sperm sacs, both extending posteriorly for several somites . . . . . *nanus* Eisen

7 (6) Sperm ducts present; penial bulbs present; diverticula of spermathecae distinct 8

8 (9) Penial glands absent; penial bulbs composed of muscle and connective tissues only; atria absent; no accessory glands . . . . . *kincaidi* Eisen

9 (8) Penial glands present within penial bulb; atria present. 10

10 (15) Atrial glands absent 11

11 (12) Accessory glands absent; atria within penial bulbs . . . . . *beringensis* Eisen

12 (11) Accessory glands present 13

13 (14) Dorsal blood-vessel arising in 19; sperm sacs extending to 16; ovisac extending to 18 *fontinalis* Eisen (See p. 185)

14 (13) Dorsal blood-vessel arising in 14–15; accessory glands very large; copulatory papillae exceptionally prominent . . . . . *pedatus* Eisen (See p. 185)

15 (10) Atrial glands present 16

16 (17) Accessory glands present; 5 atrial glands; both sperm sacs equally developed, extending to 15–16 and en-

closed in ovisac; dorsal blood-vessel arising in 13–14 . . . . . *solifugus* var. *rainierensis* Welch

17 (16) Accessory glands absent 18

18 (19) Two atrial glands; spermiducal funnels small, almost globular, wider than long, bases twisted. . . . . *eastwoodi* Eisen

19 (18) More than 2 atrial glands; spermiducal funnels cylindrical, longer than wide 20

20 (25) Two sperm sacs; no glands at ectal openings of spermathecae 21

21 (22) Sperm ducts very short, about as long as spermiducal funnels; 3–4 atrial glands; sperm sacs extending through 15 or more somites . . *penicillus* Eisen

22 (21) Sperm ducts distinctly longer than spermiducal funnels; 6–8 atrial glands 23

23 (24) Spermiducal funnel very long, extending posteriorly for 6 somites; sperm sacs beginning in 7; length 170 mm.; 105 somites . . *grandis* Eisen (See p. 185)

24 (23) Spermiducal funnels very large, length but little greater than diameter; sperm sacs arising in usual position in clitellar somites and extending to 27 or beyond; sperm ducts extending to 21; dorsal blood-vessel arising in 20 . . . . . *fuscus* Eisen

25 (20) One sperm sac, extending to 16, bifurcating at posterior end; a few glands at ectal openings of spermathecae; spermiducal funnels short, only about 1½ times longer than diameter; 1 ovisac present, extending to 16, bifurcating at posterior end, containing sperm sac; dorsal blood-vessel arising in 22–23 . . . . . *johanseni* Welch

26 (1) Spermathecae long, extending through more than 1 somite 27

27 (28) Spermathecae without diverticula; spermiducal funnels large, about 5 times longer than diameter; sperm sacs within ovisacs, extending to 15–17; 8 atrial glands; penial glands present; spermathecae extending to 7–8, no connection with digestive tract;

sperm ducts extending to 19 within ovisacs; 2 ovisacs extending to 22–26; dorsal blood-vessel arising in 18 . . . . . *altus* Welch

28 (27) Spermathecae with diverticula 29

29 (30) One small diverticulum on spermatheca; 5 atrial glands; no accessory glands; penial glands present; spermathecae not connected with digestive tract, extending to 6; 2 long sperm sacs; 1 ovisac . . . . . *asiaticus* Eisen

30 (29) Two diverticula on spermatheca 31

31 (32) Spermathecae connected with digestive tract by narrow ducts in 7–8; 12–14 atrial glands; penial glands of 1 kind only; no accessory glands . . *vegae* Eisen

32 (31) Spermathecae not connected with digestive tract . . 33

33 (34) Penial glands absent, body of penial bulbs composed of muscle fibers and connective tissue only; diverticula of spermathecae minute, globular; spermathecae extending to 10; more than 5 atrial glands; no accessory glands; dorsal blood-vessel arising in 15 . . . . . *orcae* Eisen

34 (33) Penial glands present; diverticula of spermathecae well developed, elongate 35

35 (36) One prominent accessory gland present at each penial bulb; spermathecae extending to 10–12; 8–10 small, globular atrial glands; penial glands present; dorsal blood-vessel arising in 16; sperm ducts short, but little longer than spermiducal funnels; spermiducal funnels large, length about 4 times greater than diameter, extending through 2 somites . . . . . *franciscanus* Eisen

36 (35) Accessory glands absent 37

37 (40) Not more than 10 atrial glands; body pigmentation absent 38

38 (39) Spermathecae extending into 7–8; spermiducal funnels with length about twice diameter, constricted in middle; 5 atrial glands; 2 sperm sacs extending to 18 or beyond; 1 ovisac; penial invaginations simple, undivided . . . . . *setchelli* Eisen

39 (38) Spermathecae extending to 11, crossing each other near 5/6; spermiducal funnels approximately cylindrical, length about 7 times the diameter; about 5 atrial glands; no accessory glands; no sperm sacs; 1 ovisac extending to 31–33; each penial invagination divided into an ental chamber and a similar ectal compartment, the former receiving the sperm duct; 1 set of penial glands . . . . . *hydrius* Welch

40 (37) More than 10 atrial glands; body pigmentation present 41

41 (42) Sperm ducts long, extending to 17; 16–20 small, sessile, globular atrial glands; spermathecae extending to 9–10; spermiducal funnels trumpet-shaped, length about twice the diameter, rim long and recurved; sperm sacs extending beyond 18 . . *obscurus* Eisen

42 (41) Sperm ducts short, confined to clitellar somites; atrial glands elongate 43

43 (44) Spermiducal funnels long, extending cephalad through 3 somites, length about 9 times diameter; sperm ducts about 3 times longer than spermiducal funnels; spermathecae extending to 10–11; about 16 atrial glands; sperm sacs extending caudad about 30 somites; 1 set of penial glands . . *harrimani* Eisen

44 (43) Spermiducal funnels of the usual extent, confined to 11 45

45 (46) Penial glands exclusively unicellular; spermathecal diverticula united with ampulla at its ectal end; spermathecal duct short, diverticula longer than duct; 2 small groups of glands at ectal openings of spermathecae; spermathecae extending to 9–11; spermiducal funnel 3–4 times longer than diameter; sperm sacs extending to 31–35; 1 ovisac, bifurcating in 16, extending to 35, enclosing sperm sacs . . . . . *gelidus* Welch

46 (45) Penial glands in part multicellular; spermathecal diverticula attached to middle of long spermathecal duct, diverticula shorter than duct; spermathecae extending to 7–8; no glands at ectal opening of spermathecae; 2 long sperm sacs; 1 ovisac . . . . . *maculatus* Eisen

Discussion

Mes. unalaskae. The only record of this species is the original description by Eisen (1905, pp. 20–21) based upon specimens collected at Unalaska, Alaska, Aug. 10, 1899, which are described as "not fully developed." The clitellum was absent and there appears to be reason for questioning the maturity of the sexual organs. In fact, the structure of the spermathecae and the penial bulb, as presented in Eisen's figures (text fig. 1c, e), suggests a certain degree of immaturity. On the other hand, the connection of the spermathecae with the digestive tract and the presence of well developed sperm sacs and an ovisac argues nearness to sexual maturity. However, there is, at present, no alternative other than to give the species this tentative position in the key.

Mes. fontinalis var. gracilis. Eisen (1905, p. 54) describes a new variety of this species under the name *gracilis* but the differences as described are so slight that the writer questions its validity.

Mes. pedatus. A discrepancy occurs in Eisen's original description (1905) of this species which demands notice here. In his key to the species of *Mesenchytraeus* (pp. 18–20), *pedatus* is placed under "*d. No atrial and no penial glands, but many accessory glands at the lower apex of sperm-ducts.*" In the formal description (pp. 55–57), no statement appears concerning the presence or absence of penial glands but, on plate IX, fig. 5, a figure appears representing penial glands within the small penial bulb and indicated by an abbreviation "*pb.*" No such abbreviation appears in the explanation of this figure but an abbreviation "*p. blb,*" not on the figure at all, is explained as "penial bulb containing unicellular glands." There is every reason for believing that "*pb*" on the plate is a typographical error and should have been "*p. blb.*" The writer regards the figure as indicating more correctly the structure of the penial bulb, hence the place of treatment in the key.

Mes. fuscus var. inermis. A variety of this species, described by Eisen (1905, pp. 49–50) under the name *inermis*, differs from the original species in minor respects only.

Mes. grandis. Eisen, the original describer of this species, points out (1905, pp. 46–47) the close relationship which seems to exist between it and *Mes. harrimani*, and suggests the possibility that

grandis may be identical with *harrimani*, "the spermathecae having become accidentally reduced." The original description was based upon a single specimen "which was carefully narcotized and fixed in sublimate," implying that it was in good condition. It is not clear just how a spermatheca might become "accidentally reduced" except through some unfavorable dissection or sectioning. No statement is made as to the method of preparation of the specimen for study but there is a hint that it was dissected. The sperm sacs are described as beginning "as far forward as somite VII, where they appear to spring from the septum VI/VII. They gradually increase in size posteriorly, except in the somites of the clitellum, where they are thin, even and tubular. The walls of the sperm-sacs are thick, a cross-section resembling a cross-section of a spermatheca." The anterior position, as described, of the sperm sacs is a very unusual one and, while Eisen was experienced in recognizing elongated spermathecae, the writer is inclined to raise the question as to whether the above-mentioned "sperm-sacs" in the anteclitellar somites might not have been portions of the spermathecal ampullae. If such was the case then *grandis* would fall into the group of species having elongated spermathecae and possibly might have to be regarded as the same as *harrimani*. However, definite settlement of this matter must await study of additional material.

Mes. beumeri. In the above key no account is taken of a doubtful record of *Mes. beumeri* (Mchlsn.) given by Moore (1899, p. 141) as occurring in the vicinity of Philadelphia.

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EXPLANATION OF PLATE

Abbreviations

atr	atrium
atr gl	atrial gland
div	spermathecal diverticulum
in b c'l	inner bulb cells
m	muscle tissues within penial bulb
pen b i	penial bulb invagination
pen po	penial pore
sp'r	spermatheca

Plate XVII

Mesenchytraeus hydrius n. sp.

Fig. 1. Diagram of 4–10, showing position, extent, gross structural features, and crossing of the elongated spermathecae.

Fig. 2. Penial bulb and associated structures. Somewhat diagrammatic.

Fig. 3. Penial bulb as it appears in transverse section of worm. Bulb in retracted condition.

Fig. 4. Nephridium from a postclitellar somite.

Fig. 5. Nephridium from an anteclitellar somite.

Fig. 6. Brain.

Fig. 7. Spermiducal funnel.